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WORKER SIZE AND PIRACY IN FORAGING ANTS

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Abstract.—Foraging ants (1.8 to 12 mm long) vied for small (≤3.2 mg, ≤1.5 mm) cheese baits of two sizes. Small ants succeeded in gathering only the smaller baits. Although small ants found the larger baits first ca. 50% of the time, they always lost the large baits to solitary foragers of larger species. Small baits were generally gathered by the first species to find them with the smallest (≤2 mm long) ants successful in ca. 80% of the cases. Recruitment was of no consequence in the success of these encounters. Control of baits was exchanged only to species of ants of equal, or, more often, larger size. The largest species, *Camponotus pennsylvanicus*, never foraged the small baits.

The niche of the small (<2 mm long) species of ants appeared to be defined in part by consistently unsuccessful confrontations with individual foragers of larger species for discrete food particles of a certain size range (i.e. too large or cumbersome for a solitary forager of a small species to carry easily, but easily carried by individuals of a larger species). The pirating of food items by solitary foragers may be an important part of the foraging repertoire of many medium-sized and large ants.

Key Words: baits, *Camponotus*, *Aphaenogaster*, *Myrmica*, *Leptothorax*, *Tapinoma*, *Paratrechina*

Ants exploit a variety of food resources (e.g. honeydew, seeds, and living and dead invertebrates) and, according to Carroll and Janzen (1973), forage primarily for particulate and widely scattered food items. If small enough, items are garnered by solitary foragers, while recruitment is important in foraging for items too large or cumbersome for an individual ant to carry by itself. The size of food items taken by various insect species has been found to be related to the overall size of the insect or the dimensions of its food gathering organs (Hespenheide 1973, Wilson 1975). Such size-match relationships are known among the Formicidae (Davidson 1977a, b, Bernstein 1979, Wilson 1978), but may not be universal in the family (Rissing and Pollock 1984).

Larger ants can take food particles of a greater size range than small species, resulting in overlap of dietary resources (Chew and DeVita 1980). Direct interspecific competition by foragers for large baits has been well documented (e.g. Levins et al. 1973). Field observations of single foragers of large ant species wresting food items (primarily dead arthropods) from groups of several workers of small species prompted this investigation of the frequency of this sort of competition.

Materials and Methods

Observations were made at two sets of bait stations at Beltsville, Maryland. One set of 10 bait observation sites was on an infrequently used sandy road through an upland Virginia pine, *Pinus virginiana*, and mixed xerophilous oak woods, while the second set of 10 stations was along a path through a more mesic woods of mixed hardwoods (mostly oaks). Mosses, grasses, herbs and sapling trees and shrubs grew between the wheel ruts, but there was little litter on the sandy road. The path was more shaded and leaf litter plentiful. Bait stations were a minimum of 10 m apart. Studies were conducted May–September, 1200 to 1800 h EDT.

Cheese cubes of two sizes ($\bar{x}$ = 3.2 ± 0.21 mg [n = 10] ca. 1 × 1 × 1 mm and $\bar{x}$ = 0.52 ± 0.20 mg [n = 10], ca. 0.5 × 0.5 × .50 mm) served as baits. At each station a large cube was dropped without respect to locations of foraging ants, but so that I could observe it. I observed the ensuing bait-related ant activity until the bait was carried into an ant nest. This procedure was repeated, using the smaller baits. Entrances of some ant nests were hidden beneath leaf litter. In such cases, I waited ca. 3 min after an ant with a bait disappeared in the litter, and then I brushed away the litter to find the nest entrance. The distances ants carried baits were measured. I recorded the species of ants involved in the fates of the cubes and the type and sequence of the activities. These bait drops were made in June and July between 1215 EDT and 1715 EDT with temperatures of 24 to 33°C.

Additional random drops, elsewhere along the road and in the woods brought the total number of bait stations to 31 for small baits and 29 for large baits on the road and 20 for small baits and 32 for large baits in the woods. To further verify the patterns of foraging success observed with the bait drops, additional baits were placed in the paths of foragers of species more commonly involved in the random drops. All the additional drops were between 1215 and 1800 EDT at 24–33°C, but over a longer period, May–September. While ants may exhibit species-specific patterns in their daily foraging periods, the cast of characters, observed during the daily and late May–early September time frames of this study, nevertheless remained remarkably constant. *Prenolepis imparis* (Say), a dominant species in cooler seasons was commonly seen at the sites during those times, but was never involved in the observations reported here.

The ant species were classified according to size as Class I (≤4 mm long), II (>4 and ≤8 mm), III (>8 mm). The ants were measured in an extended position from the frons to the tip of the gaster. Samples of each species were collected for identification. The species composition of the ant fauna of the wooded and road sites was similar with the pertinent exceptions that *Aphaenogaster treatae* (Forel) was strictly limited to the road, and the *A. rudis* (Emery) to a lesser degree to the woods, and that the Class III *Camponotus pennsylvanicus* (DeGeer) was also more prevalent in the woods.

The frequencies with which ant species were first to find baits and frequencies of successfully removing baits were analyzed by Chi square contingency tables. Ant specimens were identified by D. R. Smith, the U.S. Department of Agriculture Systematic Entomology Laboratory, U.S. National Museum of Natural History, Washington, D.C.

Results

Small baits both on the road and the path were never found first by the largest ants (Class III), whereas, the smallest species (Class I) were first to find both large and small baits significantly more often than the other size classes ($P < 0.05$) (Table 1). There was no significant difference ($P > 0.05$) in the frequency with which Classes II–III found large or small baits (Table 2). On only 2 of 20 occasions Class III species were the first to find the large baits.

Although Class I species were first at baits for >50% of random drops, they never succeeded in gathering a larger bait, nor did they remove fragments visible to the naked eye from the larger baits. In every instance

Table 1. The size classes of ant species which were first to find cheese baits randomly dropped with respect to foraging ants.

Subfamily	Species	Size Class	First to Find: Small Bait: Road	Woods	Total	Large Bait: Road	Woods	Total
Myrmicinae								
	Myrmica pinetorum (Wheeler)	II	2	1	3	2	1	3
	M. emeryana (Forel)	II	6	5	11	7	8	15
	Aphaenogaster rudis (Emery)	II	2	0	2	1	1	2
	A. treatae (Forel)	II	0	0	0	4	0	4
	A. sp. A	II	0	1	1	1	2	3
	Pheidole bicarinata vinelandica (Forel)	I	1	0	1	0	0	0
	P. pilifera (Roger)	I	1	0	1	0	0	0
	Leptothorax curvispinosus Mayr	I	3	2	5	2	3	5
Dolichoderinae								
	Tapinoma sessile (Say)	I	3	1	4	1	1	2
Formicinae								
	Paratrechina parvula (Mayr)	I	12	9	21	10	11	21
	Lasius alienus (Foerster)	I	1	1	2	1	0	1
	Camponotus pennsylvanicus (DeGeer)	III	0	0	0	0	2	2
	Formica pallidefulva nitidiventris Emery	II	0	0	0	0	1	1
	F. subsericea Say	III	0	0	0	0	2	2
			31	20	51	29	32	61

[a] Small bait ca. 0.5 mg, ca. 0.5 mm^3; large bait ca. 3.2 mg, ca. 1.5 mm^3.
[b] Class I ≤4 mm long, Class II >4 and ≤8 mm long, Class III >8 mm long.

solitary foragers of larger species pirated the baits from Class I ants, even when as many as 5 of the smaller ants were present. Recruitment of co-workers was of no consequence in the final outcomes of these trials. Occasionally a Class II forager relinquished a large bait to a solitary large forager of another species.

On the other hand, the ant to initially discover a small bait, usually successfully carried the bait to its nest. Class I species *Paratrechina parvula* (Mayr) successfully foraged all nine small baits it was first to find on the road and 7 of 8 of the small baits in the woods, while *Lepotothorax curvispinosus* Mayr garnered 1 of 2 small baits on the road and 2 of 3 in the woods. *Tapinoma sessile* (Say) relinquished the only small bait it found to *P. parvula*. Class II species were always successful in garnering the smaller baits when they were first to find them. For baits on the sandy road or on leaf litter along the path, the foraging success results were similar. *Myrmica emeryana* (Forel) (Class II) foragers were first to the large baits in just 3 of 20 random drops, but garnered them 10 times.

Class I species *P. parvula, L. curvispinosus,* and *T. sessile* relinquished large baits when they were first to find them in all of 20, 5 and 2 instances respectively. Whereas Class II species *M. emeryana, Aphaenogaster treatae* and *A. rudis* successfully foraged large baits on 7, 4 and 4 instances respectively. In about half the observations, three or four species of ants were involved in the fate of large baits (Table 3). Typically, when a forager of a small species (e.g. *P. melanderi*) was the first ant to find a large bait, it palpated and tugged at the bait. Unable to move the bait, the ant would repeatedly move 1 to 3 cm from the bait, only to return in a few seconds and repeat the palpating and tugging. In a few instances, the ant would

Table 2. Fates of two sizes of cheese baits foraged by three size-defined class worker ants of various species.

Bait Size[a]	Stations[b]	Size Class of Ants	No. Times First to Find Bait	No. Times Successfully Foraged Bait
Small	Road	I	7A	7A
		II	3A	3A
		III	0B	0B
	Woods	I	6A	6A
		II	4A	4A
		III	0B	0B
	Road and Woods	I	3A	13A
		II	7A	7A
		III	0B	0B
Large	Road	I	6A	0A
		II	4A	9B
		III	0B	1A
	Woods	I	4A	0A
		II	5A	8B
		III	1B	2A
	Road and Woods	I	0A	0A
		II	9A	17B
		III	1B	3A

[a] Small bait ca. 0.5 mg, ca. 0.5 mm^3, large bait ca. 3.2 mg, ca. 1.5 mm^3.
[b] Ten bait drops each on road and in woods.
[c] Class I ≤4 mm long, Class II >4 mm and ≤8 mm long, Class III >8 mm long.
[d] Numbers in the same column, pertaining to the source bait size and station, and followed by the same letter are not significantly different (Chi square contingency tables, $P < 0.05$).

leave and not return and fewer still were instances of recruitment of nestmates. However, a forager of one of the larger species generally arrived while the small forager was alone at the bait. The larger ant wandered to within about 1 cm of the bait before it turned abruptly toward the bait. The interloper often seized the bait, or when necessary, tore it from the grip of the smaller ant, and carried it directly nestward. Other times the larger ant nipped the smaller one, particularly if the latter accidentally or aggressively interfered with the larger ant seizing the bait. Such brief attacks drove away the smaller species even when two or three of them were at the bait; nor did the smaller ants pursue the interloper as it carried the cube nestward.

Table 3. Sequence of control of large baits by ant species and speed and distance baits were carried to ants' nests.[a]

Station	Sequence of Species Controlling Bait[b]	Distance Bait Carried (cm)[c]	Time Bait Carried (min)[c]	Speed Bait Carried (cm/min)[c]
Road	PP, MP, PP, AT	91	8.0	11.4
Road	PP, TS, PP, TS, PP, TS, ME	127	5.0	25.4
Road	AT	36	1.0	35.6
Road	ME	122	4.0	30.5
Road	TS, MP, TS, LC, TS, MP, MP, AT	61	1.5	40.7
Road	AT	229	2.0	114.3
Road	ME	168	8.0	21.0
Road	LC, MP, ME	86	3.0	28.8
Road	PP, ME	122	7.0	17.4
Road	PP, AT	130	0.8	155.4
Woods	CP,[d] PP, ME	196	4.5	43.3
Woods	FP,[d] LC, CP	1128	6.5	173.5
Woods	LC, ME	97	1.5	64.4
Woods	LC, PP,[e] ME	71	2.5	28.5
Woods	PP, ME	48	3.0	16.1
Woods	PP, AR	46	1.0	45.7
Woods	AS	30	5.75	5.3
Woods	FS, ME, CP	549	1.25	438.9
Woods	AR, CP,[e] AR	104	1.5	69.4
Woods	ME	117	2.5	46.7

[a] Baits ca. 3.2 mg, ca. 1.5 mm^3.
[b] Abbreviations for ant species: AR = *Aphaenogaster rudis*, AS = *A.* sp., AT = *A. treatae*, CC = *Camponotus castaneus*, CP = *C. pennsylvanicus*, FP = *Formica p. nitidiventris*, FS = *F. subsericea*, LC = *Leptothorax curvispinosus*, ME = *Myrmica emeryana*, MP = *M. pinetorum*, TS = *Tapinoma sessile*, PP = *Paratrechina parvula*.
[c] By the last ant that took control of the bait and brought the bait to its nest.
[d] Abandoned bait.
[e] Attacked ant at bait, but did not gain control.

Discussion

The 0.5–3.2 mg, 0.5–1.0 mm range appeared to be the lower limit of food particle size at which relative forager size/strength operated as a significant factor in the outcome of competitive foraging for this assemblage of ant species and type of food. Success in foraging for items smaller than this threshold size appeared to be more dependent on a forager's ability to find a food item before competitors. Unwieldiness of food items (arthropods with appendages intact) probably effectively creates the same sort of strength related barrier to foraging ants. Studies with larger baits (e.g. Levins et al. 1973, Lynch et al. 1980) suggest that there is a food item size threshold above which the largest species must resort to recruitment to efficiently exploit the item (Oster and Wilson 1978). Such large food items are therefore subject to multi-species use before one colony can dominate or later through pilfering by small species.

For large food items multi-species use is likely and small items are more apt to be gathered by individual small ants rather than very large foragers. However, there may not be a smooth ant size/bait size usage gradient between the extremes, because small ants may derive little or no food material from particles that are too large for their individual foragers to carry easily, yet which are readily pirated by solitary foragers of common large species.

In terms of energetics, it seems inefficient for a small ant to consistently compete unsuccessfully for a resource (i.e. food items like the large cheese baits). One explanation may be that the minimal quantity a worker manages to remove in her infrabuccal pocket before the food item is lost is a worthwhile payload. Also, food items of the dimensions of the large cheese baits may be scarce in natural conditions and thereby represent an abnormal situation. However, baits of both sizes did approximate the sizes of many small invertebrates, which might die of a variety of causes (e.g. drowned by a down pour). Certainly the relative size distribution of available foods is of utmost importance in the natural environment (Wilson 1975).

The pirating of food items from rather ubiquitous smaller ants by solitary foragers may be an important behavior in some larger species (e.g. *Aphaenogaster* spp., *Myrmica emeryana*). In this study, *A. treatae* successfully foraged more large baits (6) by seizing them from smaller ants, than by being the first to find them (4), while *M. emeryana* pirated 8 large baits and garnered 12 which they found first. Foragers of regularly interloping species may have been aided in detecting baits by the activity of the smaller ants already at the baits.

According to Oster and Wilson (1978), the main disadvantage to reliance on recruitment is the time it consumes. In this study recruitment occurred infrequently, and with no more than 3 to 5 workers of *P. parvula* at a bait at one time. Recruitment rates have been related to food patch size and sucrose content (Taylor 1977). Perhaps the size or content of the cheese baits used in this study were not attractive enough to elicit strong recruitment, although the small baits were gathered by the first species to find them. Lynch et al. (1980) reported that *P. melanderi* (Wheeler) showed greater recruitment to sugar baits. In the case of food items similar in size and attractiveness to large baits, it might be inefficient for small ant species to recruit and mobilize several workers only to lose virtually the entire food items to unrelated ants.

Based on their bait studies, Lynch et al. (1980) considered *P. melanderi* and *L. curvispinosus* as timid ants and *Prenolepis imparis*, an aggressive dominant speices. *P. imparis* was common at the site of this study, but since most of the trials were conducted in mid-summer, this species, which is more active in cooler weather, was not actively involved. According to Lynch et al. (1980), a single *P. imparis* worker can hold its own at a bait against the large *A. rudis*. No smallish ant seemed to fit this role in this study. A detailed investigation of paired interspecific interactions for control of small baits might explain competitive relationships in assemblages of ant species.

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